Postural Stability in Animals of Different Sizes, Shapes, and Neural Delays

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Harrison Bartlett

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Approved by:

Dr. Lena Ting, Advisor
School of Biomedical Engineering
Georgia Institute of Technology

Dr. Minoru Shinohara
School of Applied Physiology
Georgia Institute of Technology

Date Approved:

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

SUMMARY

An important issue in the area of biology is form following function. It is evident that animals have wide variation in morphology, but what functions do these forms follow?

The postural stability of an animal decreases as the neural delay increases. This delay increases with animal size because signals must travel across a longer distance at a constant speed. Despite this increase in delay, large animals typically do not fall.

In addition to the neural components, animal morphology also affects stability. Therefore it is possible that stability is a guiding principle of morphology. An animal may have a particular shape in order to function in its niche in an ecosystem while maintaining a stable morphology. It is proposed that in order to maintain postural stability, large animals have adapted different morphologies to counteract their longer neural delays. The postural stabilities of animals of different shapes and sizes will be examined using a mathematical model of balance.

The effects of neural delay and morphology on postural stability were studied using a four-bar linkage model of frontal plane balance [1] applied to previously-published morphological data from horses and dogs [2,3]. The postural stability was quantified by calculating the maximum allowable neural delay for an animal in order for the animal to prevent falling via corrective action. This measure was compared to the calculated neural delay for each animal. It was found that maximum allowable delay scales proportionally to neural delay, indicating that postural stability may scale across animal size and morphology. The model has limitations in that it does not incorporate animal width into the calculation of neural delay, therefore excluding the effects of animal width. These results may reveal a scaling relationship for the stability of biological systems across sizes, morphologies, and species.

CHAPTER 1

INTRODUCTION

An important biological issue is the matter of form-function relationships. It is evident that animals have many different morphologic differences related to postural stability such as height, stance width, length, etc. In addition to morphologic differences, aspects of neural control to achieve stability may differ across animals. For example, mammals' neurons differ with respect to axon diameter and degree of myelination, which both have minimal effects on signal speed across different mammals [8].

The neural delay of an animal increases as the efferent signal (the signal to the muscles from the nervous system) speed decreases. The control (efferent) signal delay is the distance the signal must travel (d) divided by the conduction velocity (CV) of the signal from the nervous system (t=d/CV). In larger animals, the distance (d) is larger. If CV does not change, and d becomes larger, the neural delay will become larger. It is known that CV is relatively constant across different animals [1]. This constancy across animals, irrespective of size, means that large animals have large delays. Why is it that large animals do not fall?

Morphology also affects animal stability because we know that ratios of stance width, hip width, and height affect stability [2]. Animals' nervous systems must work to control the animals' balance given the constraints of their morphologies. The efferent signals must travel through the animal in order to interact with the muscles. Because of the effect of animal dimensions on stability, one can postulate that animals may have evolved different morphologies in order to maintain an acceptable postural stability given their neural delays and CVs. *I hypothesize that the postural stability (the ability to not fall) of animals is similar across species with different physical dimensions and delays, but similar morphological proportions. I also hypothesize that postural stability scales to prevent falling equivalently within species across breeds of varying size and physical dimensions.*

Previous research in the area of animal scaling has shown relationships between animal size and behavior. For example, Biewener has examined how, as animals get larger, they must adjust their postures when standing and moving so as to not exert too much force on their bones. In this way, animal locomotion is a function of animal size and thus, animals' behaviors are greatly affected by their size [4]. Animal morphology has even been used to predict locomotor strategies for ancestral primates by taking advantage of scaling properties and their effects on motion [5]. Although relationships between animal morphology and size have been related to behaviors, the relationship between these metrics and postural stability has yet to be investigated. It is known that as an animal gets larger, its time to fall (time to hit the ground after falling) increases. larger animals also have larger neural delays. These neural delays must be short enough to allow the animal to correct its balance before falling.

To study the effects of scaling on animal stability, we used a four-bar linkage model of frontal plane balance and previously published morphological data. We specifically examined the stability of animals that differed drastically in height and width to determine which had the greatest effects on animal stability. Animal stability was quantified as the maximum allowable time delay, and this value was compared to each animal's estimated time delay. Additionally, the stable bounds for position and velocity feedback gains for the four-bar linkage system under a delayed feedback control system were calculated. The effects of animal mass, height, and width were then examined.

CHAPTER 2

METHODS

We studied the effects of neural delay and morphology on postural stability using a four-bar linkage model of frontal plane balance [1] applied to previously published morphological data from horses and dogs [2,3]. We wanted to understand how the nervous system maintains postural stability in animals of different morphologies. We quantified postural stability by calculating the maximum allowable neural delay for an animal in order for the animal to prevent falling via corrective action. We compared this measure to the calculated neural delay for each animal. We also calculated the stable bounds for the position and velocity feedback gains of the system with a delayed feedback controller. We then examined the effects of varying key model parameters on the stable bounds for the feedback gains.

Model Inputs

We obtained previously published morphological data from horses and dogs and used these data to modify a four-bar linkage model previously used for frontal plane balance in humans [2,3,1]. A visual depiction of the model can be seen in Figure 1.

To analyze the stability of these animals, we calculated the maximum allowable time delay for each animal and compared it to an estimate of actual time delay for that same animal. To perform these calculations, the model required the following parameters: S (stance width), W (hip width), H_{com} (Height of the center of mass from the top of the leg), L (the leg length), I_{trunk} (moment of inertia of the trunk), I_{leg} (moment of inertia of the leg), m_{leg} (mass of the leg), m_{trunk} (mass of the trunk), and L_{com} (height to the CoM of the leg). Of these parameters, W and L could be taken directly from the previously published data [2,3] while the remaining parameters had to be estimated. The previously published data contained morphological information for 1155 dogs from 109 different breeds and 1215 horses from 65 different breeds. The estimated parameters were calculated using the morphological parameters found in the previously obtained data.

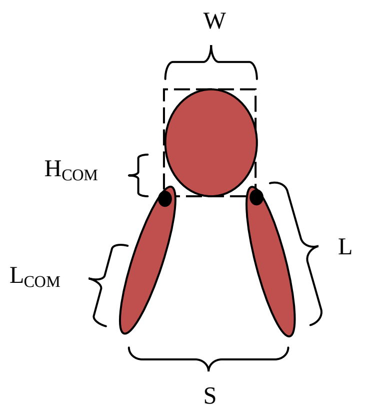

Figure 1: Four-bar linkage model of frontal plane balance. The four bars are the upper body, the legs, and the ground.

To estimate S, a ratio of S:W of 1.01 was applied to all the animals, implying that stance width is proportional to hip width at a fixed ratio. This ratio was used to generate the initial model outputs that were later plotted. H_{com} was estimated as W/2 in both dogs and horses. This estimation assumes that the chest of dogs and horses is circular. The leg length of the horse was taken to be the distance between the bottom of the hoof and the point of the elbow; the leg length of the dog was taken to be the distance between the free epiphysis of the accessory carpal bone to the greater tubercle of the humerus.

Mass Estimation

Individual Animal Masses

The mass terms were also estimated because the previously published data did not include this information. To estimate mass terms, the average density for horses and dogs were calculated. To calculate the average density of a horse, the average mass of a Clydesdale was divided by the estimated average volume of the Clydesdale horse [6]. This volume estimate was taken by assuming that the horse is roughly a cylinder with a measured circumference C and a body length d (Figure 2). The volume of this cylinder is then $C^2d/4\pi$. We estimated horse density as 0.4 kg/in^3 using a cylinder-based model. To calculate the average density of a dog, the average mass of a greyhound was divided by the estimated average volume of the dog [7]. This volume estimate was calculated assuming that the dog is roughly a rectangular prism defined by the dimensions of the chest and the length of the dog. The rectangular prism model was used for the dogs because we were able to obtain more specific morphological data pertaining to the animals' torsos, allowing us to make a better estimate of the animals' shapes. The density of 0.0282 kg/in^3 was used for the dogs and the volume of the dogs was estimated using the prism-based model. Density was multiplied by body segment volume to obtain respective body segment masses. The accuracy of the density estimates was later analyzed by comparing the estimated animal masses to measured average animal masses.

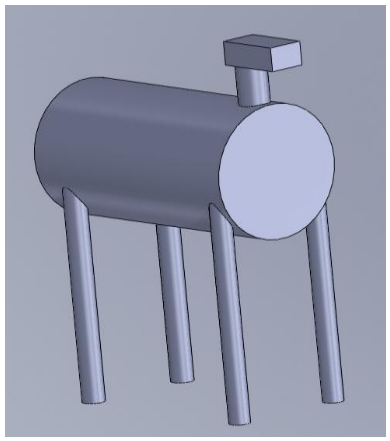

Figure 1: Visual depiction of the cylinder-based model of the dog and horse for body segment volume calculations.

The moment of inertia terms were also estimated. The moment of inertia of the leg was calculated by treating the leg as a slender rod rotating about the body's center of mass. The moment of inertia of the body was estimated by treating the body of the animal as a cylinder rotating about its own center of mass.

Generalized Animal Masses

When calculating the stable bounds for the system's feedback gains, animal mass was again estimated. The stable feedback gains of the system are the position and velocity feedback gains to be input into a linearized delayed feedback of postural control (seen visually in figure 1) that allow the system to remain stable (the real part of the system's eigenvalues are all less than zero).In addition tocalculating the time to fall for each animal individually, the stable feedback gain bounds were also calculated for representative animals. To determine the mass of the representative animals, a range of masses for each of the four breeds of interest (Bulldog, Italian Greyhound, Thoroughbred, and Clydesdale) were determined. Additionally, ranges for the animals heights, widths, and other morphological data were determined from the raw morphological data provided by Brooks and Sutter [2,3].

Mathematical Model

The difference in stance width and hip width, δ, was then calculated for each animal using Equation 1. Next, a parameter, η, consisting of a commonly recurring expression was calculated using Equation 2.

$$\delta = S - W \tag{1}$$

$$\eta = \frac{1}{2}\sqrt{4L^2 - \eta^2} \tag{2}$$

Using these two simplifying terms the effective inertia about the center of mass (I_e) for each animal could then be calculated using Equation 3.

$$I_e = 2(M_{leg}L_{com}^2 + I_{leg}) + \frac{1}{W^2}[m_{trunk}(H_{com}\delta - W\eta)^2 + I_{trunk}\delta^2] \tag{3}$$

The gravitational stiffness (G_e) of each animal was also calculated using Equation 4. This term incorporates the effects of gravitational forces acting on the system.

$$G_e = [\frac{m_{trunk}(H_{com}\delta^2)}{W^2} - \frac{(2L_{com}m_{leg} + Lm_{trunk})(\delta\eta^2 - L^2S)}{LW\eta}]g \tag{4}$$

After calculating both the effective inertia and gravitational stiffness, the maximum allowable time delay (τ_{max}) for each animal could be calculated using Equation 5. This calculation was done under the assumption that the horse and dog system were acting under a delayed feedback controller [1]. The maximum allowable time delay represents the maximum allowable neural delay for an animal in order for the animal to prevent falling via corrective action [1].

$$\tau_{max} = \sqrt{\frac{2I_e}{G_e}} \tag{5}$$

This τ_{max} is the maximum allowed value for the delay in the system's equation of motion shown in Equation 6.

$$Ms^2 - K + (k_p + k_v s)e^{-\tau s} = \varnothing \tag{6}$$

Equation 6 also contains position and velocity feedback gains (k_p and k_v respectively). The stable bounds for these feedback gains were calculated as done in Bingham 2011 [1]. These bounds represent the possible combinations of k_p and k_v in which the system remains stable (the real part of the system's eigenvalues are all less than zero).

Stability Analysis

Time to Fall

To analyze the each animal's stability, the maximum allowable time delay was compared to the animal's estimated neural delay. The maximum allowable time delay (time to fall) metric incorporates aspects of the animal's shape such as hip width and stance width. The neural delay metric incorporates aspects of the animal's nervous system.To do this comparison, each animal's actual neural delay was calculated by dividing the total distance the neural signal must travel (twice the height of the animal because the signal must travel from the ground to the brain and back) by the neural conduction velocity and adding this time to the electromechanical delay. The electromechanical delay is defined as the amount of time it takes for a muscle to produce force after it has been reached by a neural signal. The neural conduction velocity used for the horses and dogs was 2204.72 inches/second (55.99 meters/second) [8] and the electromechanical delay used was 0.065seconds [9]. The neural conduction velocity of the horse and dog was calculated as the average of the neural conduction velocities of a shrew and an elephant due to the size of a horse and dog in comparison to these large and small animals[8].

The maximum allowable time delay and actual neural delay were then compared for each animal via a scatter plot. All of the data pertaining to the horses and dogs for which measurements had been collected were plotted in order to examine how the size and shape of different animals affected their stability. Additionally, a regression analysis was run on these data in order to apply a best-fit line to this data set.

The important characteristics for comparing the stabilities of the animals (Tau_max, Ie, Ge, and delay) were noted for 4 different animals: Italian Greyhound (skinny), Bulldog (wide), Thoroughbred (skinny), and Clydesdale (wide). These animals were chosen because the skinny and wide breeds in each species have almost identical height, but very different widths. These important parameters were calculated at 2 different S/W ratios: S/W=0.5 and S/W=1.5 to examine the effects of stance width on these parameters (S/W =1.01 was used for initial results and the S/W ratio was then varied to create a comparison table across stance width).

Stable Bounds for Feedback Gains

The stable bounds for the feedback gains of the system (Eq 6) were calculated and the effects of changing animal mass, height, and width were determined. The stable bounds for the feedback gains were determined based on the appendix (Eq 13 and 14) of Bingham 2011 [1].To determine the effects of varying an individual parameter on the stable range of feedback gains, two of the three parameters (mass, height, and width) were set to the average value for a particular animal. Then, the third parameter was varied and the changes to the range of stable feedback gains were observed. Each of the three parameters were varied independently to determine their individual effects on the stable range of feedback gains.

The parameters were varied in two different ways: by percentage or across the feasible range of values. The parameters were varied by percentage to examine the mathematical parameter sensitivities, but were varied across the feasible ranges of values to determine the realistic effects of mass, height, and width on stability. These two ranges are not equivalent because an horse height may vary by 50% across a breed while width may only vary by 10% across the same breed. When a parameter was varied by percentage, the stable set of feedback gains was calculated four times: (at an initial value of mass/height/width, at a 10% increase from the initial value, at a 20% increase from the initial value, and at a 30% increase from the initial value). It was also important to observe the effects of realistic variation of each of these model parameters. Because of this, each parameter was varied across a feasible range of values that are realistic for the animals being simulated. When the varied parameter was varied across the feasible range of values, a minimum and maximum mass/height/width were determined and this range was divided into ten values to be tested. The stable range of feedback gains was then calculated and plotted at each of these ten values. Then, the stable bounds for the feedback gains of a Clydesdale and a Thoroughbred with different masses and heights were compared to examine how differences in one parameter such as mass may be compensated for by differences in another parameter such as height to produce similar feedback gain bounds despite morphological differences.

CHAPTER 3

RESULTS

We analyzed our estimate of individual animal masses to determine the accuracy of our choice of animal density. The average calculated mass of a Thoroughbred horse was 651.55 ± 78.24 kg compared to a measured value for this average of 499 kg [6]. For the Clydesdale, we found the average mass to be 899.13 ± 90.97 kg compared to the measured value of 997.9 kg [6]. These estimates could be skewed because of the very rough volume estimates that were made for the horses. The average mass of the bulldog was calculated to be 22.27 ± 13.43 kg compared to the previously collected value of 23.5 kg [7]. The average mass of the greyhound was calculated to be 6.30 ± 1.58 kg compared to the previously collected value of 31.5 kg [7]. The drastic difference in the mass calculations for the greyhound may be due to the fact that the dog is skinny and its legs come up to a very high point on the dog's chest; therefore, the prism-based model for dog volume drastically underestimated the dog's volume. These discrepancies pose a limitation to the accuracy of the model.

Time to Fall

The maximum allowable time delay for each animal was plotted against the actual animal delay in a scatter plot (Figure 3). The x axis in this plot is the animal's actual neural delay, which is directly proportional to the animal's height. The y axis on this plot is the animal's time to fall which incorporates other aspects of the animal's shape such as hip width and stance width. The best-fit regression lines for the dog data and horse data were both plotted over the data. Both dogs and horses were represented in this plot. The maximum allowable time delay represents the relative stability of the animal, while the actual delay correlates very highly with height of the animal (total delay is comprised of both transmission delay based on height and electromechanical delay) . As can be seen in the Figure 3, there is a high correlation between actual animal delay and max allowable time delay.

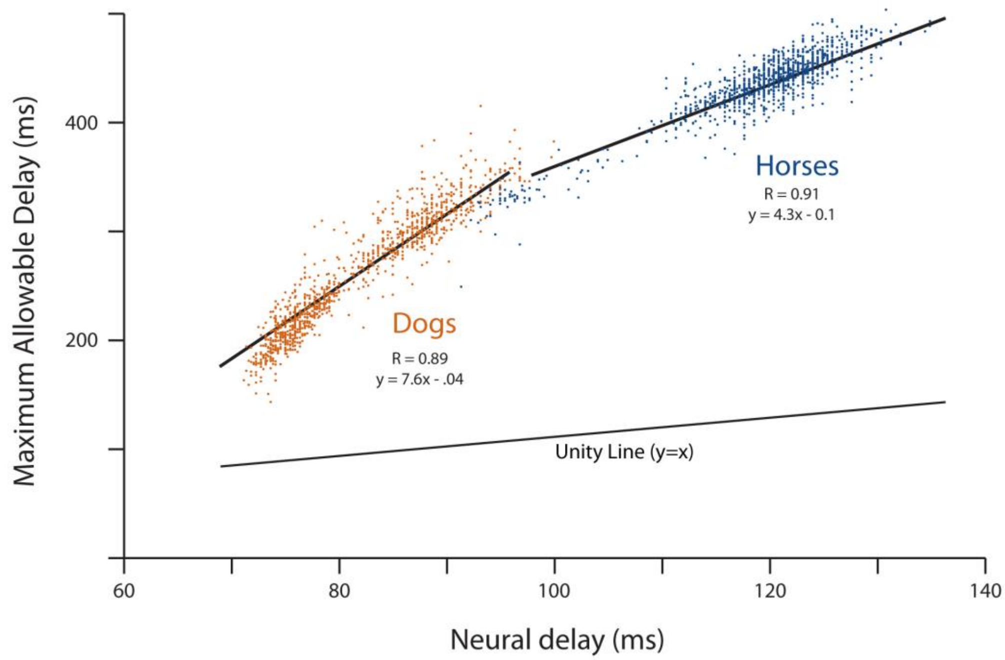

Figure 3: Plot of Maximum allowable delay vs. actual animal delay. Best-fit regression lines are shown in blue. Dog data is shown as red asterisks while horse data is shown as blue asterisks. The unity line is also plotted for comparison with the best-fit regression lines

Important characteristics for animal stability can be seen in Table 1. In this table, the values were calculated once with S/W equal to 0.5 and once with S/W equal to 1.5 to determine the effects of stance width on these parameters. These values give a good idea of how stance width affects animal stability and also allows for the comparison of different animals' delays.

	Tau_max (ms)		Ie (kg in^2)		Ge (kg in^2)		Delay (lambda)(ms)	
S/W	0.5	1.5	0.5	1.5	0.5	1.5	0.5	1.5
Italian Greyhound	0.247	0.209	813	578	2.61*10^4	2.64*10^4	0.0784	0.0784
Bulldog	0.275	0.186	3.34*10^3	1.51*10^3	9.28*10^4	9.72*10^4	0.0789	0.0789
Thoroughbred	0.483	0.396	1.19*10^6	8.05*10^5	1.02*10^7	1.03*10^7	0.122	0.122
Clydesdale	0.508	0.416	1.98*10^6	1.35*10^6	1.53*10^7	1.55*10^7	0.129	0.129

Table 1: Indicates the key parameters in the stability analysis for 4 animals. The numbers are presented as (S/W=0.5) / (S/W=1.5). The breeds chosen are a skinny dog (Italian Greyhound), a wide dog (Bulldog), a skinny horse (Thoroughbred), and a wide horse (Clydesdale).

Stable Bounds for Feedback Gains

The stable bounds for position and velocity feedback gains for a Bulldog are plotted in Figure 4. This figure shows the effects of varying animal mass, height, and width by percentage up to 30% in 10% increments on the range of stable feedback gains. As mass and height increase and as width decreases, the range of stable feedback gains increase with height being the most sensitive parameter. The D-shaped region bounded in the plot represents stable combinations of position and velocity feedback gains for the system.

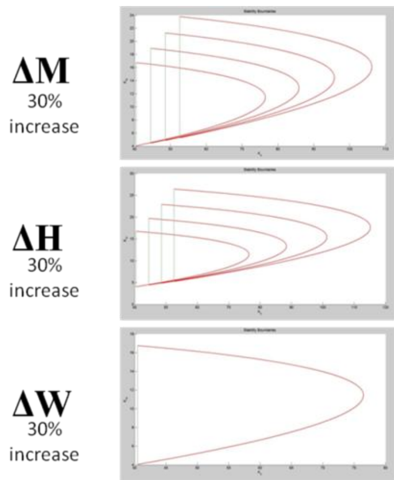

Figure 4: Stable ranges of position (x-axis) and velocity (y-axis) feedback gains for a Bulldog with mass, height, and width independently varied up to 30% in 10% increments. The range of stable feedback gains increase with increasing mass and height. The ranges increase when bulldog width is decreased.

The ranges of stable feedback gains were also examined as the mass, height, and width of animals were varied across a feasible range of values for each animal. The effects of this variation can be seen in Figure 5. As seen in Figure 4, height remains the most sensitive parameter.

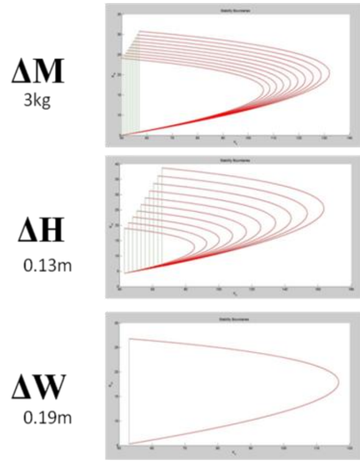

Figure 5: Stable ranges of position (x-axis) and velocity (y-axis) feedback gains for a Bulldog with mass, height, and width independently varied across feasible ranges for Bulldogs (1/10th of the range at a time).

The ranges of stable feedback gains for a Clydesdale and Thoroughbred are shown in Figure 6. The masses, heights, and widths of these two simulated horses are listed in Table 2. These two animals have very similar ranges of stable feedback gains despite having different morphologies (the Thoroughbred is taller and wider than the Clydesdale, but the Clydesdale is heavier.)

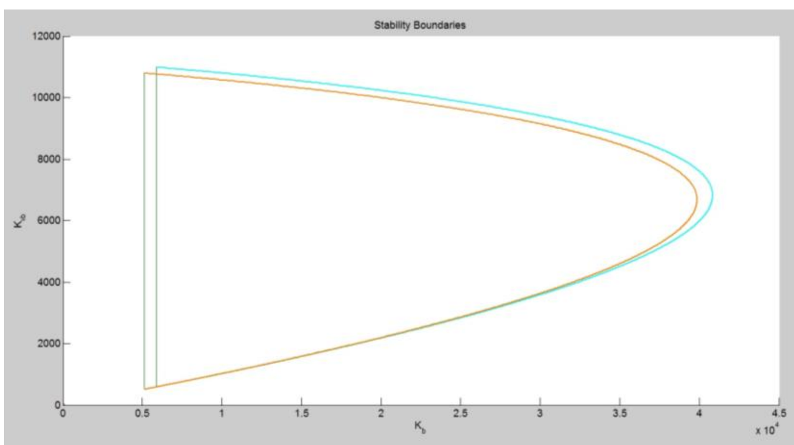

Figure 6: Stable ranges of position (x-axis) and velocity (y-axis) feedback gains for a Clydesdale (turquoise) and Thoroughbred (orange).

	Thoroughbred (Orange)	Clydesdale (Turquoise)
Mass (kg)	524	680
Height (m)	1.75	1.63
Width (m)	0.53	0.41

Table 2: Morphological Characteristics of Simulated Thoroughbred and Clydesdale Masses, heights, and widths of the simulated Thoroughbred and Clydesdale plotted in Figure 5.

CHAPTER 4

DISCUSSION

Time to Fall

The high correlation between actual animal delay and max allowable time delay (seen in Figure 3) implies that as an animal gets larger, it's time to fall also increases linearly, meaning that large animals have a longer time to react to perturbations in order to remain standing. Because of the linear relationship between the neural delay and time to fall, it shows that as an animal gets larger and their neural delay gets larger, the large animal can afford the larger delay as shown by the increase in their time to fall. The actual neural delay (the x axis in Figure 3) represents the effects of the nervous system on stability. The time to fall (the y axis in Figure 3) represents other aspects of the animal's shape and morphology. The relationship between these two metrics helps to give an idea of how an animal's morphology and nervous system interact to maintain stability. We observed a strikingly similar relationship in both species, indicating that stability is conserved both within species and across species of different sizes and shapes. It is interesting to note a section of overlap in the plotted data showing that similarly sized horses and dogs have nearly identical stabilities.

If the neural delay were longer than the time to fall, then the animal would not be stable. In the case of these animals, the neural delay is not in any danger of approaching the mechanical limits of stability. The linear relationship seems to suggest that there may be a consistent "safety factor" for the mechanical/nervous system stability. This is represented graphically by the vertical distance between the unity line and the best fit lines on the data.

The results of this study indicate that large animals may be more passively stable (able to stay standing with less necessary neural control) than small animals. This result is shown by the larger distance in Figure 1 between the best fit line and unity line for larger animals than for smaller animals. The larger distance indicates that large animals have difficulty with active balance control due to their long delays. Therefore, they must rely on passive stability. However, small animals do not have much time to react to perturbations due to their lower maximum allowable time delays. One possible solution to this problem is for smaller animals to adopt a crouched posture. This crouched posture acts like a spring and damper, which will allow small animals more time to react to perturbations. In a crouched position, the coactivation of muscles provides a spring-damper-like system to absorb shocks or perturbations. This position is seen in nature in which large animals keep their joints fairly straight and small animals maintain crouched postures.

The vertical distance between the unity line and particular points on the plot gives us an idea of the relative stability of an animal. For instance, in examining the data, we found that Clydesdales are more stable than thoroughbreds because their wide shape provides more passive stability, despite having similar delays. Similarly, we found that bulldogs are more stable than greyhounds for the same reasons. These results can be seen in Table 1 in the Tau Max column.

Stable Bounds for Feedback Gains

As shown in Figure 4, variations in height have the greatest effect on the stable range of feedback gains for the four bar linkage model. Variations in mass have the second most effect while variations in width do not have much effect at all. It was also important to examine the effects of varying these parameters over a feasible range of animal masses, heights, and widths. For example, if height is the most sensitive parameter, but Bulldog masses vary much more than Bulldog heights, mass may still be the most important parameter for Bulldogs in terms of determining their stable ranges of feedback gains. As seen in Figure 5, variations in height still had the greatest effect on the stable ranges of feedback gains.

The finding that height is the most important factor is counterintuitive because the range of mass should be drastically larger than the range of heights for animals because mass scales by height to the third power. Despite the large range of masses, the sensitivity of height was still determined to be the most important factor for determining the stable range of feedback gains. Width was determined to be the least sensitive parameter for determining stable ranges of feedback gains. This finding is intuitive because the four bar linkage model can be viewed as two inverted pendulums roughly in parallel. If this is the case, changing the distance between the two inverted pendulums (width), will have very little effect on the system's stability.

The results of parameter sensitivity analysis yield some interesting implications. As seen in Figure 6, two different breeds of horses with different morphologies and physical characteristics have similar bounds for their feedback gains. As seen in Table 2, the Thoroughbred is lighter, taller and wider than the Clydesdale but the two animals have similar stable ranges of feedback gains. In this case, it seems that the difference in heights is compensated by the difference in masses of the two animals to yield similar stable ranges of feedback gains.

Model Limitations/Conclusions

There are a few issues to address in terms of the accuracy of this model. One possible flaw in the model is that variations in animal width are not incorporated into delay. However, the most probable case is that width is a very small component of the delay because variations in animal height are much more drastic than variations in width, so even though an increase in width causes a neural signal to travel a longer distance, this increase in distance is minor in comparison to variations in height.

Another possible limitation is that the animals analyzed have been bred over time to preserve desired morphological characteristics. This deliberate breeding may limit the degree to which the results of this study can be applied to animals found in nature. Although the breeding of animals may affect the robustness of the results, it will only limit the results in a minor way assuming that the breeding process has not altered the physical shapes of the horses and dogs drastically from when they were found in nature.

These results may reveal a scaling relationship for the stability of biological systems across sizes, morphologies, and species. These results could help to elucidate some form-function relationships that are evident in biological systems.

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